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Stand Features and Height Growth in a 36-Year-Old Maritime Pine (Pinus Pinaster Ait.) Provenance Test

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Summary

A trial comparing 10 maritime pine provenances was measured at age 36 years. Ranking for vigour remained stable throughout the test period. Two major groups were obvious, Atlantic lowland seed sources with high vigour and frost resistance and southern seed sources with low vigour and low frost resistance. Three provenances had intermediate features. Height growth curves were fitted with a non-linear growth model and the shape of the curves (relative height of the inflexion point) was almost the same for all provenances. The asymptote and the maximum growth rate were correlated at the provenance level but not at the individual phenotypic level. This indicates a good juvenile-mature correlation for seed source vigour. The results for growth characteristics were compared to previous findings concerning the structure of genetic variability and the physiological features of provenances. The growth potential of Maritime pine seed sources appeared to be mostly a result of natural selection for drought resistance.

Key words: provenance test, *Pinus pinaster*, height growth curves, non-linear regression.

Résumé

Un test de comparison de 10 provenances de Pin maritime situé à Mimizan (Landes) a été mesuré à l'âge de 36 ans. Le classement pour la vigueur est resté stable pendant la période de test. Les provenances peuvent être classées dans 2 groupes principaux : d'une part les provenances atlantiques de plaine qui sont vigoureuses et résistantes au froid et d'autre part des provenances méridionales qui sont peu vigoureuses et sensibles au froid. Trois provenances ont des caractéristiques intermédiaires. L'ajustement des courbes de croissance en hauteur d'arbres dominants avec un modèle non linéaire montre que les courbes des différentes provenances ont pratiquement la même forme (paramètre de forme = hauteur relative du point d'inflexion). L'asymptote et la vitesse de croissance maximale sont corrélées au niveau des moyennes de provenances, mais pas au niveau phénotypique individuel. Ceci indique une bonne corrélation juvénile-adulte de la vigueur des provenances. Les résultats sont comparés à ceux obtenus précédemment concernant la structuration de la variabilité génétique dans l'ère de répartition et certaines caracteristiques physiologiques des provenances. Le poten-

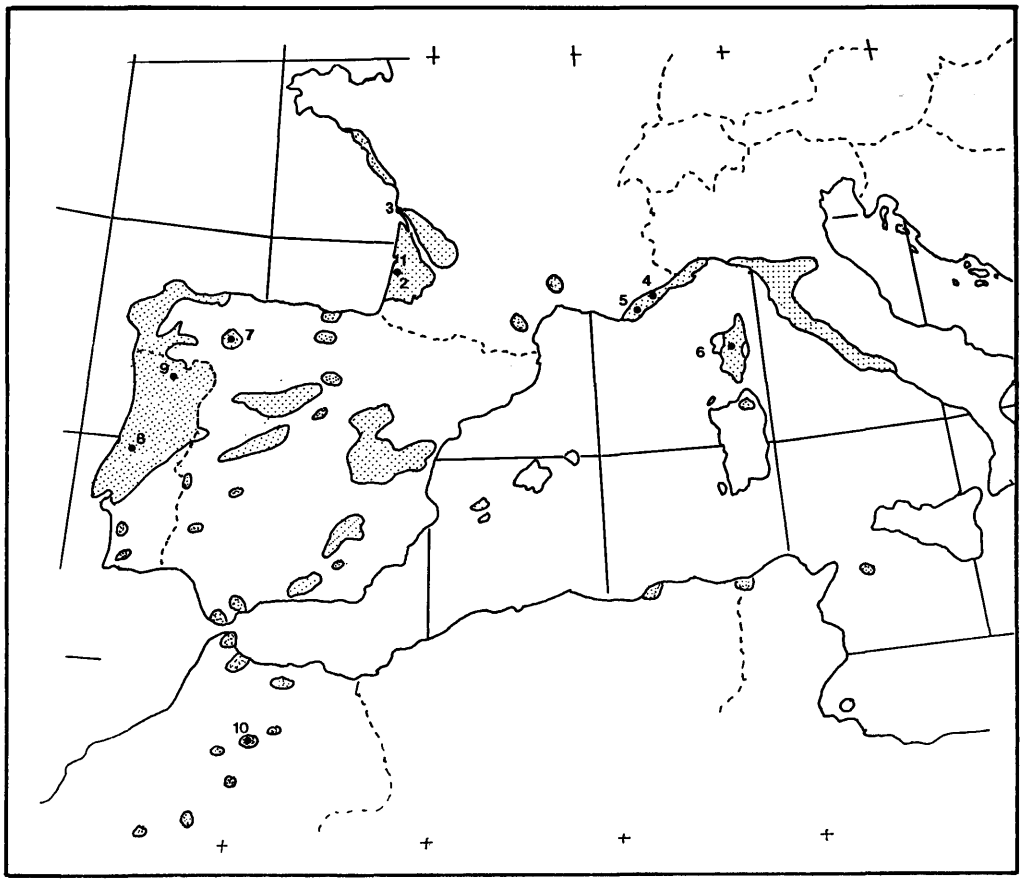

Figure 1. — Natural range of maritime pine (from BARADAT and MARPEAU, 1988) and location of provenances represented in the study.

tiel de croissance des provenances de pin maritime est surtout le résultat de la sélection naturelle pour la résistance à la sécheresse.

Mots-clef: provenance, *Pinus pinaster*, courbe de croissance en hauteur, régression non linéaire.

Introduction

Maritime pine *(Pinus pinaster* AIT.) is one of the most important forest tree species in France, covering about 1 million hectares of intensively managed, even aged stands in the south-west (the "Landes" forest). In order to provide improved trees for this forest, a recurrent selection program was begun within the local provenance (BARADAT and PASTUSZKA, 1990). This program started with mass selection of 550 plus trees from the Landes area, selected for volume, stem straightness, and branching habit. The 3rd selection cycle is now beginning and intraspecific variability from Corsican provenances is being used to improve stem straightness. The choice of the local provenance was based especially on early results of a provenance trial established between 1952 and 1955 in Mimizan (Landes), where 10 seed sources were compared.

The natural range of maritime pine is in the occidental Mediterranean basin and the South European Atlantic coastal zones (*Fig. 1*). With a size of 1500 km x 2000 km, this area is smaller than that of other major European or American forest species but covers a wide range of climates with dry and wet conditions and spanning an altitudinal range of 2000 m. The geographical pattern of genetic variation of this species was investigated by BARADAT and MARPEAU (1988) and BAHRMAN *et al.* (1992).

In the Landes area, some studies were made in 9-year-old maritime pine provenance tests and focused on physiological features (GUYON and KREMER, 1982) and on the analysis of height growth components (KREMER and ROUSSEL, 1986). The growth characteristics of the Mimizan test were studied at age 10 (ILLY, 1966 and 1967). We measured this test in 1991. Since rotation age in the coastal Landes area is around 60 years, a study at age 36 years provides a valuation of the mature characteristics of each seed source.

This study has 2 main objectives:

(1) an assessment of provenance growth characteristics at a rather mature age;

(2) an analysis of genetic variability of height growth curves at the provenance level using a modelling technique.

Height was analysed because it is a good measure of vigour and is less influenced by competition than diameter growth. Compared to classical growth analysis, modelling provides a synthetic overview of the growth process. In some provenance tests changes of ranking occur (CONKLE, 1973; MAGNUSSEN and PARK, 1991). These changes are difficult to describe and interpretation is not obvious. NAMKOONG and CONKLE (1976) divided growth curves into 3 periods: exponential growth, constant growth, and declining growth. I fitted a non-linear sigmoïd function to growth curves data (DANJON and HERVE, 1994). The results of growth curve analysis are more synthetic and are easy to interpret, provided that the precision of the estimation is acceptable. Precision was assessed by examining bivariate plots of parameters with approximate confidence ellipses. Measures were carried out at the stand level and

Table 1. — Geographic data for the 10 tested provenances (following ILLY, 1966). Elev. = elevation in m; Prec. = precipitation in mm/yr.

Name	Locality	Region	Land	Latitude	Longitude	Elev.	Soil	Prec.
1 Mimizan	Mimizan	Landes	France	44.1°N	1.1°W	30	sand dune	950
2 Coastline	Mimizan	Landes	France	44.1°N	1.1°W	0	sand dune	950
3 Tremblade	La Tremblade	La Coubre	France	45.4°N	1.1°W	50	sand	770
4 Estérel	Péguière et Maraval	Estérel	France	43.5°N	6.9°E	320	sandy clay	800
5 Maures	Les Mayons	Maures	France	43.3°N	6.4°E	300	micaschist	700
6 Corsica	Restonica	Corte	France	42.2°N	9.1°E	750	sandy soil on granite	870
7 Spain	El Pinar de Tabuyo	Léon - Astorga	Spain	42.5°N	6.2°W	1000	sand	-
8 Leiria	Leiria	Leiria	Portugal	39.5°N	8.5°W	30	sand	800
9 Tras-os-Montes	Serra do Padrela	Tras-os-Montes	Portugal	41.4°N	7.4°W	1300	podzol on granite	1300
10 Morocco	Tamrabta	Sefrou, Moyen-Atlas	Morocco	33.3°N	5.0°W	1750	leached soil on sandstone	850

the growth curves study was made on a sample of the dominant trees.

Material and Methods

Material

The „Malgaches" provenance test is located in the State Forest of Mimizan, at 1.5 km from the ocean, on a well drained sandy podzol in the stabilized dune area on a relatively flat site (for details see ILLY, 1966). The ground water level is fairly deep, giving rise to summer drought. Ten seed sources were planted in 34.5 m x 34.5 plots in 1.5 m x 1.5 m spacing and 4 randomized replications. The plot size is large, so the number of replications is low.

The provenances sampled cover a large part of the species natural distribution, but the sample size is small (*Table 1* and *Figure 1*). The Mimizan seed source was sampled close to the test site. The Coastline seed source was sampled a few kilometers from Mimizan in a protection zone established in the early 19th century to stabilize the coastal sand dunes. The Tremblade stand is located near the ocean, north of the Landes area. The Maures and Estérel seed sources come from Provence, a mountainous region of southeast-France with a Mediterranean climate. Only the Leiria seed source and the seed sources originating from the Landes area come from low elevation zones.

Sowing ranged from spring 1952 to spring 1955 and seedlings were planted 6 months later. Reinforcement plantings were made throughout this period, the age of the trees is consequently not precisely known. A hard frost occurred in january 1956 (minus 13 °C), leading to severe damage. Frost resistance was assessed in 1956 by survival count, the number of remaining trees per plot ranged from 90 to 400. Seed sources originating from southern areas suffered more severely (ILLY, 1966). Another hard frost occured in 1985. Selective thinnings were carried out in 1971, 1974, 1981 and 1987 (respectively an average of 15%, 35 %, 10 % and 30 % of the remaining trees were cut).

The data were collected in spring 1991. Stand features were assessed with an inventory of all diameters at breast height (dbh) and with a dendrometer height measurement of 5 dominant trees per plot (randomly chosen in the 30 % trees with greatest diameter). To analyse the height growth curves, 2 additional dominant trees per plot were felled for each provenance in the 2 blocks with best growth (because the stocking was low on some plots in the 2 other blocks). Butt angle of lean and dbh were measured before felling. Then height increments and polycyclism were measured by using branch whorls as morphological markers (KREMER, 1981a). Maritime pine produces either 1 or 2 and even 3 growth cycles per year, each cycle terminated by a whorl. Polycyclism was analysed as 2 variables:

— FPOLY: frequency of 2nd flush (lammas shoot);

— LPOLY: relative length of 2nd shoot; i. e., mean ratio (2nd shoot length/annual shoot length) for years in which the tree produced a 2nd shoot.

These percentages were transformed to arcsine for variance analysis.

Growth curve analysis

The framework of growth curve analysis was defined in DANJON (1992) and DANJON and HERVE (1994), a software designed by HERVE was used for the fitting. The growth curve data were fitted to a 4 parameter non-linear model with a convenient reparametrization to gain stable estimations, according to ROSS (1970).

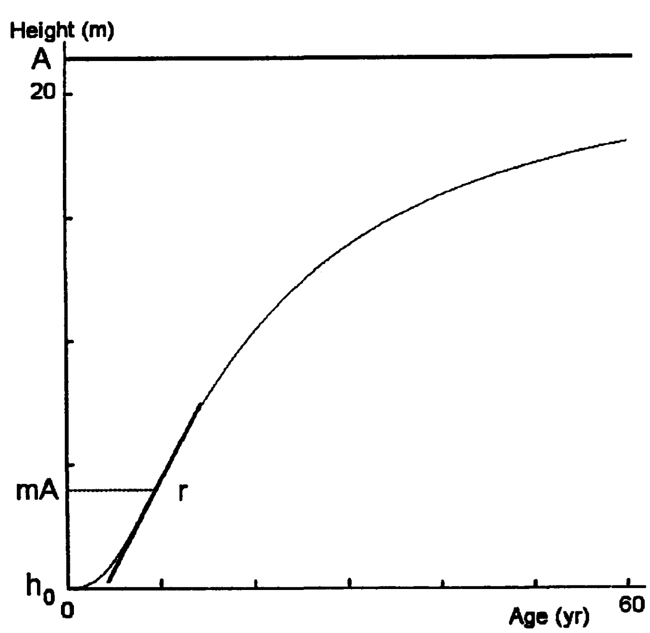

Figure 2. — Diagram showing the meaning of the growth curve parameters (LUNDQVIST-MATERN function with the following average estimations: A = 21.4 m; r = 71.8 cm/yr; m = 0.185 and h_0 = 0.27 cm).

The LUNDQVIST-MATERN function (h = height and t = time) (MATERN, 1959):

$$h(t) = A\exp\text{-}[\frac{gt}{m} + (\log\frac{A}{h_0})^{-1/n}]^{-n} \quad (1)$$

was reparametrized with m instead of n and r instead of g:

$$m = \exp-\left(1+\frac{1}{n}\right) \quad (2)$$

and:

$$r = gA\exp\left[\left(1+\frac{1}{n}\right)\left(\log\left(1+\frac{1}{n}\right)-1\right)\right] \quad (3)$$

The 4 parameters are A (asymptote), r (maximal growth rate), m (shape parameter, i. e., relative height of the inflexion point) and h_0 (height at time 0) — (*Fig. 2*). With this reparametrization, all 4 parameters have direct physical meanings.

As stressed by DAY (1966), to obtain precise estimations, for some of the parameters only 1 value should be estimated for the entire set of curves ("global parameters"). The growth trajectory being fairly complete, it should be possible to estimate up to 3 parameters for each curve (3 "local parameters"), h_0 was fixed since the age of the trees was known. Following DANJON and HERVE (1994), the CHAPMAN-RICHARDS function (RICHARDS, 1959) was fitted to the data with 3 local parameters (A, r and m) whereas the LUNDQVIST-MATERN function was used with 2 local parameters (A and r).

Provenance mean estimates of m (shape parameter) were only significantly different for the Tremblade provenance which had a low value of m. Moreover, plots of the asymptote and maximal growth rate estimates with approximate 95% confidence ellipses show that the estimation with 3 local parameters is very imprecise with high correlations among the estimates for most of the curves: these correlations averaged more than 0.8, reaching 0.94 between r and m. With 2 local parameters, the mean correlation between estimates of A and r is 0.4. The precision of estimation can be appreciated on the bivariate distribution with approximate confidence ellipses (*fig. 3*). The increase of the residual sum of squares by global estimation of the shape parameter was 20 % which was not considered excessive. Therefore, the LUNDQVIST-MATERN function was used for analysis, with a global estimation of m (m = 0.185). We should note that rankings with 2 local parameters are rather similar to those with 3 except for Tremblade: for this seed source, the global estimation of m slightly underestimates A and overestimates r. The initial slope of the LUNDQVIST-MATERN model is a little too low, a better fitting of the beginning of each curve was obtained with a very low positive value for h_0: the global estimate of h_0 yielded 0.27 cm.

Table 2. — Degrees of freedom for the 2 variance analyses.

	Stand level	Felled trees
Sample	40 plots	40 trees
Provenances	9	9
Blocks	3	1
Interaction	-	8
Error	27	21
Total	39	39

Analyses of variance

Separate analyses were made on the mean stand values for each of the 40 plots and on measures of the 40 felled trees (*Table 2*).

The model has 2 fixed factors (provenance effect: P_i, block effect: B_j) and an interaction ($(P.B)_{ij}$):

$$Y_{ijk} = \mu + P_i + B_j + (P.B)_{ij} + e_{ijk} \quad (4)$$

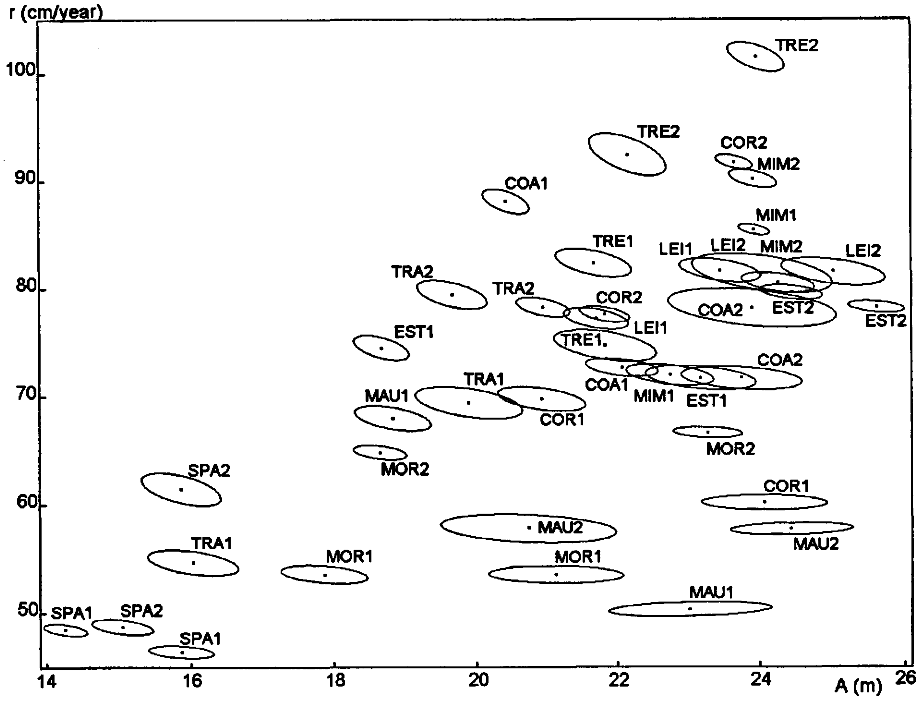

Figure 3. — Bivariate distribution of asymptote (A) and maximal growth rate (r) with approximate 95% confidence ellipses. For each tree, the 3 first letters are for the provenance and the least character for the block number.

Table 3. — Analysis of variance results and multiple stage tests for the stand level characters. Statistical significance is indicated as follows: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Provenances with same vertical bar are not significantly different at a 5% level. m. s. = mean square; Prov. = provenances.

	1956 survival	Number of trees	Mean dbh (cm)	Dominant height (m)	Basal area/plot (m²)
Prov. m. s.	729.6	336.3	21.9	13.67	2.72
Blocks m. s.	222.4	106.6	34.39	8.50	1.17
F-ratio Prov.	4.08**	5.67***	8.90***	18.3***	10.1***
F-ratio Blocks	1.25	1.80	14.0***	11.4***	4.32*
	72.5 Trembl.	67.3 Trembl.	28.6 Mimizan	16.6 Mimizan	4.34 Mimizan
	63.7 Coastl.	66.0 Spain	27.8 Leiria	16.3 Trembl.	4.27 Trembl.
	63.5 Mimizan	65.3 Mimizan	27.8 Trembl.	14.8 Leiria	3.64 Leiria
	61.5 Corsica	64.0 Morocco	27.0 Coastl.	14.5 Coastl.	3.53 Morocco
	58.5 Morocco	59.8 Corsica	26.2 Tras-os.	13.6 Tras-os.	3.40 Coastl.
	53.5 Spain	58.5 Coastl.	25.9 Morocco	13.5 Estérel	2.82 Corsica
	48.7 Estérel	57.8 Leiria	24.4 Maures	13.3 Maures	2.66 Tras-os.
	39.7 Maures	48.0 Estérel	24.1 Corsica	13.2 Corsica	2.44 Spain
	37.7 Leiria	47.0 Tras-os.	23.5 Estérel	12.6 Morocco	2.22 Estérel
	30.5 Tras-os.	40.8 Maures	21.1 Spain	10.2 Spain	2.01 Maures

(with Y_{ijk}: individual observation; μ: grand mean; e_{ijk}: residual error)

Multiple-stage tests were made with the REGWF procedure in the SAS-STAT software (SAS Institute, 1989). This test controls experimentwise error rate under partial null hypothesis and maximum experimentwise error rate under complete or partial null hypothesis.

The correlations based on provenance means and on adjusted values of each individual deviation from its provenance mean value were computed for felled trees. Correlations on adjusted individual values are phenotypic intra-provenance correlations. Correlations between provenance means reflect, in a crude way, genetic provenance effects (Velling and Tigerstedt, 1984).

Results

Plot means

Vigour was assessed by mean diameter and dominant height. Frost mortality was scored in 1956 and 1964 (in 1964 only the provenances from Portugal were damaged with 3 % mortality — Illy, 1966). The number of 1990 remaining trees per plot reflects both the survival and the vigour in the plot: in well stocked plots, the number of trees was diminished by thinning; in the other plots, the number of trees was just reduced by mortality. It can be hypothesized that the mortality rate after 1964 is especially related to freeze tolerance. The small differences in mean diameter were a result of compensation induced by competition: competition effects were high in well stocked plots and low in poorly stocked plots.

Provenance effects were highly significant for all characters. Examining rankings (*Table 3*), 4 groups can be made:

1. Provenances with a high 1956 survival, a high number of trees per plot, a high mean diameter, and a high dominant height. These well growing and frost resistant trees were from Atlantic, low-elevation provenances (Mimizan, Tremblade, and Coastline). Despite its low 1956 survival, the Leiria provenance can be added to this group, examining its mature stand characteristics.

2. Provenances with a rather low 1956 survival, a small number of trees per plot, average dominant height, and low diameter with regard to the stocking. These trees were not vigorous and had a low level of cold resistance (Tras-os-Montes, Maures and Estérel provenances).

3. The Spanish provenance had very poor vigour but an average number of trees, forming a group with low growth potential and an average frost resistance.

4. The variability of Corsican and Moroccan provenances was high. They had a rather good 1956 survival, a rather high stand density, and fairly low vigour. They were intermediate between group 1 and group 2, with average vigour and average frost resistance.

Group 2 and 3 had a low mean basal area per plot. It was high in group 1 and intermediate in group 4. Examining the height/diameter ratio, it appeared that the Morocco and Spain provenances were stockier than the other ones. It must be noticed that all trees were not of the same age. The age of felled trees could be measured, providing unbiased results.

Felled trees

No significant differences were found for angle of lean. The dune area where the test is located was not a good test environment to assess this character. The ground water level is low, providing better rooting than in the interior part of the Landes area. However, Illy (1966, and 1972 unpublished data) observed a better stem straightness of the Corsican provenance in this test.

Height rankings for age 10, 20 and 36 years remained roughly stable (*Table 4*). Rank changes arise for Tras-os-Montes and Spain seed sources, which had a better early growth period. Differences between provenances were not significant for the latter growth period (20 yrs to 36 yrs height increment).

Provenance effects were highly significant for lammas shoot frequency (FPOLY). In general, provenances from group 1 had a fairly low frequency of lammas shoots. It was often higher for provenances from group 2, but rankings did not really correspond to geographic zones. The high polycyclism of the Corsican provenance should be noted. However, in a more wet location, between the 4th and the 9th year, the Landes provenance averaged one third more lammas shoots than the Corsican seed sources (Kremer and Roussel, 1986). The provenance effect for

Table 4. — Analysis of variance results and multiple stage tests for characters measured on the 40 felled trees. All height measurements are in meters except r (cm/yr). Values for FPOLY (frequency of second shoot) and LPOLY (relative length of second shoot) were untransformed.

	Height at age 10	Height at age 20	Height at age 36	10-20 yr height incr.	20-36 yr height incr.
Prov. m. s.	3.39	9.03	13.33	2.50	0.92
Blocks m. s.	3.51	11.54	19.24	2.32	0.98
Interaction m. s.	1.30	0.99	0.74	0.21	0.25
F-ratio Prov.	6.79***	10.7***	17.7***	9.38***	2.27
F-ratio Blocks	7.02*	13.7**	25.6***	8.68**	2.42
F-ratio Inter.	2.58*	1.17	0.98	0.79	0.63
	6.02 Tremblade	12.1 Tremblade	16.8 Tremblade	6.80 Coastline	4.92 Leiria
	5.20 Mimizan	11.8 Mimizan	16.6 Mimizan	6.58 Mimizan	4.84 Mimizan
	5.09 Leiria	11.4 Leiria	16.3 Leiria	6.58 Estérel	4.77 Maures
	4.81 Tras-os-M	11.4 Coastline	15.6 Estérel	6.32 Leiria	4.68 Tremblade
	4.55 Coastline	11.1 Estérel	15.5 Coastline	6.28 Corsica	4.45 Estérel
	4.53 Corsica	10.8 Corsica	15.2 Corsica	6.07 Tremblade	4.39 Corsica
	4.52 Estérel	9.7 Tras-os-M	13.8 Tras-os-M	5.45 Morocco	4.14 Coastline
	3.29 Morocco	8.7 Morocco	13.1 Maures	5.27 Maures	4.10 Morocco
	3.21 Spain	8.3 Maures	12.8 Morocco	4.93 Tras-os-M	4.05 Tras-os-M
	3.06 Maures	7.4 Spain	10.5 Spain	4.16 Spain	3.13 Spain

	FPOLY	LPOLY	Max. growth rate (r)	Asymptote (A)	Predicted height at 60
Prov. m. s.	0.124	0.00442	470	21.0	15.0
Blocks m. s.	0.288	0.00003	619	29.9	24.0
Interaction m. s.	0.053	0.00196	81	1.26	0.4
F-ratio Prov.	11.31***	1.35	10.78***	6.82***	14.55***
F-ratio Blocks	26.24***	0.01	14.21**	9.69**	23.16***
F-ratio Inter.	4.88**	0.60	1.86	0.41	0.42
	0.72 Corsica	0.32 Spain	87.7 Tremblade	23.7 Mimizan	20.0 Mimizan
	0.68 Estérel	0.30 Tras-os-M	82.0 Mimizan	23.6 Leiria	19.8 Leiria
	0.59 Morocco	0.28 Morocco	80.4 Leiria	23.0 Estérel	19.4 Tremblade
	0.52 Tremblade	0.27 Mimizan	77.6 Coastline	22.6 Corsica	19.2 Estérel
	0.46 Spain	0.25 Estérel	76.0 Estérel	22.5 Coastline	19.0 Coastline
	0.43 Tras-os-M	0.24 Tremblade	74.8 Corsica	22.4 Tremblade	18.8 Corsica
	0.43 Mimizan	0.22 Maures	70.4 Tras-os-M	21.8 Maures	17.0 Maures
	0.35 Maures	0.22 Corsica	59.6 Morocco	20.2 Morocco	16.4 Tras-os-M
	0.25 Coastline	0.22 Coastline	58.5 Maures	19.1 Tras-os-M	16.4 Morocco
	0.13 Leiria	0.21 Leiria	51.3 Spain	15.3 Spain	12.8 Spain

the relative length of the second shoot (LPOLY) was not significant.

Height growth curves

The curve fitting was satisfactory: all growth patterns could be fitted with only 2 local parameters. The variance of the residuals was rather high at the beginning of curves (*Fig. 4*) but there was no general evidence to indicate that the LUNDQVIST-MATERN model was inappropriate for these data. The confidence ellipses were small (*Fig. 3*). A high maximum growth rate (r) was never associated with a low asymptote (A), some trees have a low r and a fairly good A. As time points are closely spaced, rather high serial correlations of residuals can be observed (*Fig. 4*). According to BATES and WATTS (1989), failure to account for autocorrelation have little effect on the parameter estimates but it results in confidence intervals which are too small.

The provenance and block effects were high for A and r. The local provenance (Mimizan) had the highest A, but only 2 provenances (Tras-os-Montes and Spain) were significantly different from Mimizan for this parameter. Spain, Maures, Morocco and Tras-os-Montes seed sources had a low A and a low r. Estérel and Corsica have a high A and r, joining group 1 for dominant height growth curves (*Fig. 5*).

Correlation between traits

For some traits, the correlation based on provenance means and the correlation based on the adjusted individual values were not consistent (*Table 5*).

There was no relation between the frequency of polycyclism (FPOLY) and any vigour character at the provenance level; a slight positive correlation with r appeared at the individual level. There was no correlation between growth and the mean relative length of the 2nd shoot (LPOLY) at the individual level. LPOLY and FPOLY were not correlated.

The ranking of provenances for dbh at age 36 years correlated significantly with height.

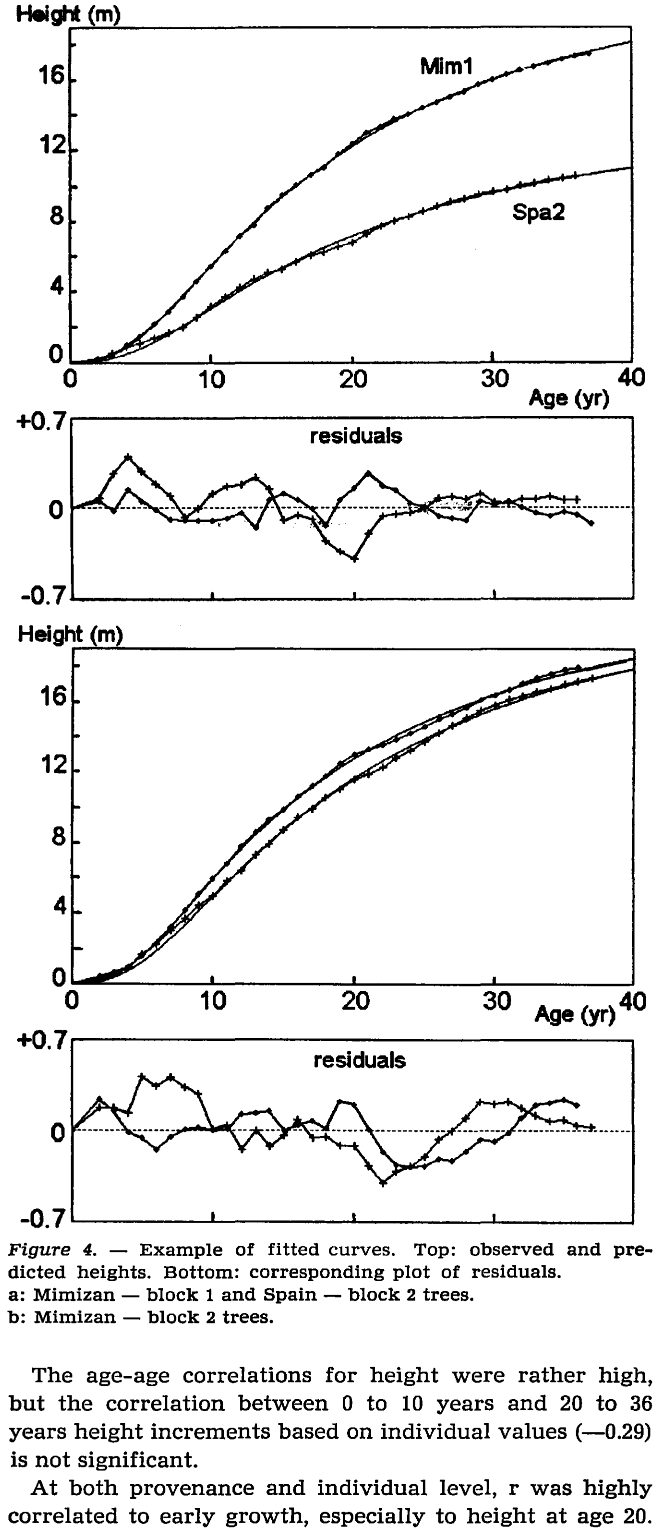

Figure 4. — Example of fitted curves. Top: observed and predicted heights. Bottom: corresponding plot of residuals.
a: Mimizan — block 1 and Spain — block 2 trees.
b: Mimizan — block 2 trees.

The age-age correlations for height were rather high, but the correlation between 0 to 10 years and 20 to 36 years height increments based on individual values (—0.29) is not significant.

At both provenance and individual level, r was highly correlated to early growth, especially to height at age 20. On the other hand, r was not correlated with 20 to 36 years height increment at the individual level. The opposite can be noted for A. There was no correlation at the individual level between A and r, but a moderate correlation at the provenance level (*Fig. 6*). The estimated height at age 60 was more correlated to later growth especially at the provenance level.

These correlations point to a low juvenile-mature correlation at the individual level and a better juvenile-mature correlation at the provenance level for height growth.

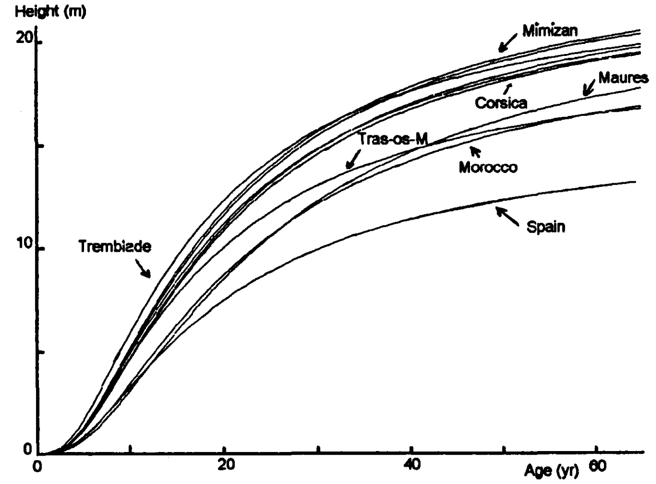

Figure 5. — Mean predicted height growth curves for each provenance.

Discussion

Despite the low number of repetitions and of provenances, this trial is interesting for its plot size and because of its advanced age. Because the plots are large, bad growing provenances are not suppressed by the good growing local provenances, allowing the expression of very different growth patterns throughout growth-harvest cycle, as in pure stands. The age gives insight to the final production values and to juvenile-mature correlations. For a more precise assessment of differences among provenances in group 1, the trial with more replications used by Kremer and Roussel (1986) should be studied in a few years.

Frost resistance

The 1991 survival rankings (roughly infered from the number of remaining trees) were similar to the frost survival rankings measured in 1956 (Illy, 1966), except for the Leiria provenance. The frost resistance of maritime pine was assessed on an earlier test with no replications ("Les Arrouilles" established 1926 — Illy, 1966) with rather the same results. In the Landes forest, a great number of stands originating from Portugal or Galicia were damaged during the frost of 1985 (Alazard, 1986), but in the present test, the Leiria provenance was not heavily damaged. The test is poorly discriminating because it is close to the ocean where frosts are not as severe (—12 °C in 1985 versus —15 °C to —25 °C in the interior part). The frost resistance of the Moroccan provenances is related to its elevational origin. Alazard (1986) observed that Moroccan seed sources originating from elevations over 600 m sustained low frost damage in 1985. The same holds for the Spanish provenance. However, the Tras-os-Montes seed source also originates from a fairly high elevation but is not frost resistant.

Individual variability in frost resistance seems to be rather high in the provenances with low freezing tolerance, because no provenance was totally eliminated by frost. Frost may have also slowed down the growth of some trees without killing them, reducing the growth potential of provenances with low frost tolerance. In any case, for practical use in the local breeding program only frost resistant seed sources should be kept.

A positive correlation between vigour and frost resistance was also found by Bariteau (1992) in *Pinus hale-*

Table 5. — Correlation matrix for characteristics of the felled trees. Upper: individual values adjusted to provenance mean. Lower: provenance mean.

	dbh(36)	h(10)	h(20)	h(36)	Δ10-20	Δ20-36	FPOLY	LPOLY	A	r
Age 10 height	0.21 0.73*									
Age 20 height	0.36* 0.81**	0.86** 0.90**								
Age 36 height	0.39* 0.86**	0.67*** 0.86**	0.85*** 0.98***							
Age 10 to 20 height increment	0.37* 0.72*	0.10 0.59	0.59*** 0.88***	0.61*** 0.89***						
Age 20 to 36 height increment	0.10 0.76*	-0.29 0.51	-0.18 0.66*	0.35* 0.79**	0.10 0.67*					
FPOLY	0.20 0.08	0.25 -0.03	0.33* -0.03	0.32* -0.07	0.25 -0.02	0.01 -0.18				
LPOLY	-0.04 -0.45	-0.14 -0.39	-0.2 -0.59	-0.22 -0.67*	-0.16 -0.68*	-0.06 -0.73*	-0.03 0.35			
A	0.23 0.80**	-0.08 0.56	0.24 0.82**	0.65*** 0.90***	0.59*** 0.92***	0.80*** 0.91***	0.20 -0.08	-0.11 -0.79**		
r	0.35* 0.81**	0.91*** 0.95***	0.98*** 0.99***	0.84*** 0.97***	0.46** 0.81**	-0.16 0.66*	0.33* -0.06	-0.20 -0.58	0.21 0.78**	
Age 60 height (predicted)	0.33* 0.85**	0.3 0.73*	0.60*** 0.93***	0.89*** 0.97***	0.70*** 0.94***	0.61*** 0.86**	0.30 -0.07	-0.16 -0.74*	0.91*** 0.97***	0.66*** 0.92***

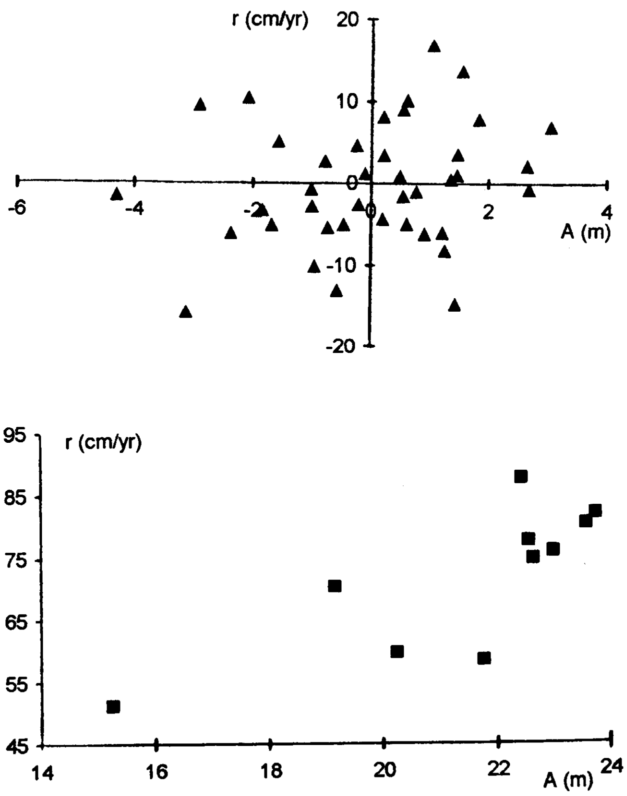

Figure 6. — Plot of asymptote (A) versus maximal growth rate (r). Upper: adjusted individual values. Lower: provenance means.

pensis Miller in southeast-France and by Magnussen and Yeatman (1988) in *Pinus banksiana* Lamb.. Vigour, then, is an expression of global adaptation of genotype to the local environment conditions (Bariteau, 1992).

Polycyclism

The variability of mean relative length of second shoot (LPOLY) seems to be low within the natural range of maritime pine: in Mimizan, between 1 year and 36 years, lammas shoots averaged approximately 25 % of annual shoot length. Kremer (1981a) showed that in progeny tests of the Landes provenance, FPOLY and LPOLY are independent and stability in space and time was better for FPOLY than for LPOLY. The expression of polycyclism depends on the environmental conditions, frequency of polycyclism is higher on wet sites (Kremer, 1981a). On wet sites, all genotypes express polycyclism, whereas in dry locations some genotypes are polycyclic in favourable years, others are polycyclic each year (Kremer, 1981b). Since frequency of 2nd shoots is a highly heritable trait (Kremer, 1981a; Danjon, 1992), assessment was precise and genetic differentiation should be easily recognized.

FPOLY tended to be higher for provenances from dry areas. In southwest-Oregon, *Pseudotsuga menziesii* (Mirb.) Franco seed sources originating from drier zones also have a greater frequency of 2nd flushing (Loopstra and Adams, 1989). It may be an adaptation to intermittent moisture availability during the growing season: trees can cease active growth temporarily when moisture is limiting, but reflush to continue growth during favourable periods (Loopstra and Adams, 1989). Lammas shoot frequency also shows a clinal variation with latitude in *Picea sitchensis* (BIROT and CHRISTOPHE, 1983) and in *Pinus banksiana* (RUDOLPH, 1964). In general, polycyclism seems to reflect adaptation to moisture and temperature gradients, this relation is weak in maritime pine.

For the provenance means, there is no correlation between the frequency of 2nd shoots and height growth. This interprovenance correlation was nonsignificant for KREMER and ROUSSEL (1986) on 9-year-old maritime pines, but was positive for BIROT and CHRISTOPHE (1983) on 8-year-old *Picea sitchensis* and for HARRINGTON (1991) on 35-year-old *Pinus taeda* L..

At the intraprovenance individual level, there was an indication of a slight positive correlation of FPOLY with early height growth (approximately through the 20th year). KREMER (1981a) observed a positive correlation between height growth and frequency of second shoots between 5 years and 12 years in the Landes provenance of maritime pine, and BIROT and CHRISTOPHE (1983) found a similar correlation for 8-year-old *Picea sitchensis*. On the other hand, there was no correlation with height increments after age 20. In the same way, this correlation seems to be null or negative in progeny tests of the maritime pine Landes provenance, at the genetic level (DANJON, 1992).

Growth curve study

The major result concerning the genetic variability of growth curves in maritime pine is that provenances originating from distant parts of the species range have similar growth patterns with the height of the inflexion point located at a value about $^1/_5$ of the asymptote. This early growth flush can be related to the ecological features of the species studied: maritime pine is an early successional, shade-intolerant species which establishes rapidly on open sites.

Working with parameters that have a precise meaning and an influence on a limited part of the curve make it possible to characterize each growth period. From correlations with height and height increments, one can see that asymptote (A) is an expression of the latter growth period (after 20 years) whereas the maximum growth rate (r) accounts for the juvenile growth period. Additionally, since the correlation between estimates of A and r for each curve are low, the PEARSON correlation between A and r in the studied set of curves was not biased by the modelling structure. The reliability of analysis results depends on the modelling procedure: several studies have been made concerning the height growth curves in *Pinus taeda*, but correlated estimates and a lack of direct physical meaning of the parameters may have clouded the analyses (MAGNUSSEN and PARK, 1991).

Modelling provides information about the asymptotes of height-growth curves, giving indications on the further evolution of rankings. For example, in a 29-year-old *Pinus ponderosa* LAWS. provenance test, NAMKOONG and CONKLE (1976) observed stable rankings between age 12 and age 29. Examining their figure representing mean provenance growth curves, one can assume that some curves will cross soon after age 29. Such changes in rank should have been characterized by a modelling procedure. However, predictions of height must be examined very carefully: the extrapolation of height to age 60 was made, but this variable gives only qualitative indications on the evolution of rankings till the clearcut. This prediction holds only under the hypothesis of a general regularity of curves. The classifications for height at age 60 years are nearly the same as for the asymptote (A) but are more discriminant. It should be noticed from a former study (DANJON, 1992) that extrapolations with 2 local parameters are much more reliable than extrapolations with 3 local parameters.

Using the height at age 60 prediction, the provenances from the atlantic group and the Corsica and Estérel provenances were expected to have the best final height. But if frost tolerance and dbh at age 36 were taken into account, it appears that the Estérel, Leiria and Corsica provenances should not be used in Landes area.

Differences between provenances are more pronounced for the maximal growth rate (r) than for the asymptote (A). The height growth increment between age 20 and age 36 is not significantly different between seed sources. In other provenance studies (NAMKOONG and CONKLE, 1976; MAGNUSSEN et al., 1985; SPRINZ et al., 1987; HARRINGTON et al., 1991) height differences between provenances have also become statistically less well defined with time. This may be partly related to the magnitude of growth between age 20 and age 36; the mean annual height increment is less than 30 cm whereas the maximal growth rate averaged 72 cm.

The nonsignificant correlation between A and r for adjusted individual values (+0.2) reflects the poor intraprovenance juvenile-mature correlation for height increments. Approaching 0.8, the (A,r) correlation of provenance means indicates that slow growing provenances have an overall poor adaptation throughout their life. In one plantation of the *Pinus ponderosa* elevational transect study, NAMKOONG and CONKLE (1976) also observed a positive juvenile-mature correlation for seed source means, a negative correlation for family means, and no correlation for the error term; this trend may originate from the intraprovenance variability for resource allocation to roots, since soil moisture becomes a strongly limiting resource after age 20.

Ranking of provenances

The comparison to the age 10 years results of ILLY (1966) indicates a general stability of rankings for height growth and vigour: group 1 provenances (Atlantic Coast) were the best adapted through the 36th year and there was no indication of a change after age 36. Major rank changes occured for the Moroccan provenance, which ranked very low at age 10 but were average by age 36. The opposite was observed for the Spanish seed source. There is some discrepancy between the results of ILLY (1966) and our results concerning height at age 10: perhaps because our sampling for growth curves included only dominant surviving trees and was made in the 2 best blocks.

A general stability of rankings between seed sources through the age of 30 was also observed by MAGNUSSEN et al. (1985) in *Pinus banksiana*, whereas important rank changes were reported by PARK and FOWLER (1983) and MAGNUSSEN and PARK (1991) for height and diameter growth of *Larix leptolepis* GORD. provenances. In the *Pinus ponderosa* transect study, stability of rankings depends on the test site (CONKLE, 1973).

Differences between groups are stable and hold for almost all vigour variables, which may be explained by major physiological differences. Vigour differences are due to adaptation to drought (GUYON and KREMER, 1982): trees originating from dry areas have a reduced physiological activity (interruption of transpiration early in the day to maintain sap pressure) and a higher inter-annual stability. These provenances have the same growth whatever the growth conditions, whereas Atlantic coast provenances have an increased growth if environmental conditions are permissive. Growth conditions are better in Mimizan than in most of the other parts of the natural range, this may explain the superiority of atlantic provenances in this test.

The greatest vigour differences may be primarily related to drought resistance, since water supply is the major limiting factor in the Mediterranean basin. Conversely, frost resistance was not associated with a lower growth potential in the Landes area. The bad vigour of the Tras-os-Montes seed source which originate from a very wet region was not expected, perhaps this provenance have suffered from summer drought.

Relation with genetic markers

The study of the structure of genetic variability by terpenes (BARADAT and MARPEAU, 1988), by isozymes, and by 2 dimensional electrophoresis (BAHRMAN et al., 1992) revealed a division in 3 major groups resulting from genetic drift during quaternary glaciations:

(1) The Atlantic group in which 6 of our studied seed sources were incorporated. Inside this group, the Spanish and Tras-os-Montes seed sources are very distant from the Mimizan, Tremblade, Coastline and Leiria seed sources and are close to the Perimediterranean group.

(2) The Perimediterranean group (Corsica, Maures and Estérel seed sources).

(3) The North-African group (Morocco seed source).

This classification was only partly in accordance with classification based on growth traits and frost resistance: the poor growth of Spanish and Tras-os-Montes seed sources can be partly attributed to genetic drift, and inbreeding in small populations (BARADAT and MARPEAU, 1988). Our Spanish source (Leòn) originates from stands which were regularly destroyed by fires and after regenerated from seed. Their growth pattern and an early and abundant flowering (ILLY, 1966) may be an adaptation to this special environment. The average performance of the Moroccan seed source was not expected, its performance may be due to its high-elevation origin. For GUYON and KREMER (1982) the same discrepancy arose for a Tunisian provenance which was found to have the same physiological features as provenances from the Atlantic group, whereas the Tamrabta Moroccan provenance has a very different physiological behaviour (GUYON and KREMER, 1982) and a special height growth architecture (KREMER and ROUSSEL, 1986) compared to the other provenances. This can be explained by the location of the Tunisian stand in a wet region (precipitation: 1050 mm/yr — BAHRMAN et al., 1992).

The growth of seed sources sampled at short distances can be different: the Estérel and Maures seed sources were sampled about 30 km apart. Leiria, Tras-os-Montes and Spanish seed sources also originate from a restricted area. Genetic differences within regions can be explained by a combination of natural selection and seed introduction: Estérel and Maures originate from a zone with rugged topography; the Leiria seed source was sampled at low elevation and Tras-os-Montes at high elevation and, in addition, the Leiria stand may originate partly from an introduction of genetic material from France (BAHRMAN et al., 1992). Among the provenances from the Landes Massif, genetic variation for growth potential is low: this area is flat, sandy, and maritime pine is the major forest species. In addition, most Landes stands are from artifical afforestation of moor lands with local provenances, which tend to prevent differentiation.

Conclusion

As vigour can be easier related to environmental seed origin than to the genetic distance between groups, and using GUYON and KREMER's (1982) results, it can be hypothesized that the growth potential of maritime pine seed sources is largely a result of natural selection for drought resistance. In addition, artificial introductions for 2000 year (due to the distribution of maritime pine in a area of early human activity), special environmental conditions (such as frequent forest fires for Spanish seed source), and genetic drift (parts of the naturel distribution are split in small fragments) may have also accounted for the seed source variability.

For the Landes area, founding the breeding program on the local provenance based on early tests was efficient because:

1. The juvenile-mature correlations at the provenance level are good.
2. The homogeneity of the Landes area is great and no significant provenance x location interactions occur in maritime pine (MATZIRIS, 1982).
3. Frost resistance is of primary importance in the Landes area.

For other breeding zones, given the importance of natural selection, attention should be directed principally to adaptation to climatic conditions, especially frost and drought resistance and growth potential which seems to be related to the water supply.

The growth of the Corsican provenance is of special interest due to its superior stem straightness and branch characters. Thus a hybrid variety between Corsican and Landes pines is being developed to improve stem straightness, mainly for wet sites (BARADAT and PASTUSZKA, 1990). This provenance has a good frost resistance and a good vigour in the 2 best block, but had a bad vigour in the 2 other blocks, which explain its bad rankings for stand level vigour. The Corsica provenance seems to be bad adapted to the Landes poorest sites. Eventhough it is expected to have a better stem straightness, the interprovenance hybrid will have significantly slower growth than the local provenance in poor conditions, unless it exhibits heterosis. However, conifers generally lack hybrid superiority (MAGNUSSEN and YEATMAN, 1988): hybrids are often better than the biparental mean but grow more slowly than the best parent. Nevertheless, hybrids may be valuable because they can broaden ecological adaptability or disease resistance.

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Buchbesprechungen

Waldbau auf soziologisch-ökologischer Grundlage. 4., teilweise neubearbeitete Auflage. Von H. Mayer. 1992. Gustav Fischer Verlag, Stuttgart und New York. ISBN 3-437-30684-7. XXVI und 522 Seiten mit 185 Abbildungen und 25 Tabellen. Gebunden DM 98,—.

Die 3. Auflage von 1984 war offenbar so schnell vergriffen, daß eine vollständige Neubearbeitung des Buches nicht möglich war. So beschränken sich die Änderungen auf einzelne Teile und hier vor allem auf eine Neufassung des Kapitels über Waldschäden unter dem Titel „Die Auswirkungen der neuartigen Waldschäden (sog. Immissions-Waldsterben) auf den Wirtschafts- und Schutzwald" (20 Seiten). Im übrigen ist der Text weitgehend identisch mit dem der vorigen Auflage. Das ist bedauerlich, da somit auch die Literaturzitate nicht über 1983 hinausgehen, nur bei den Waldschäden reichen sie in einzelnen Fällen bis etwa 1989/1990. Der „Waldbau auf soziologisch-ökologischer Grundlage" ist dennoch ein wichtiges Lehrbuch, voll von Fakten, für deren Darstellung vom Autor oft stenogrammartige, doch gut lesbare Formulierungen verwendet wurden. Von der Fülle der verarbeiteten Informationen zeugt das 52seitige Literaturverzeichnis. Das Werk gliedert sich in 6 Hauptkapitel mit zahlreichen Unterpunkten, die die Suche nach bestimmten Themen bereits über das Inhaltsverzeichnis ermöglichen. Hinzu kommt noch ein ausführliches Sachregister. Themen der Hauptkapitel sind die waldbauliche Standortbestimmung, die waldbauliche Beurteilung der mitteleuropäischen Baumarten, die Waldpflege, die Waldverjüngung, spezielle Betriebsarten sowie abschließend ein waldbaulicher Ausblick. Zu genetischen Fragen findet man leider nur gelegentlich einzelne Hinweise. Hier würde man sich in einer Neuauflage eine stärkere Berücksichtigung wünschen. Zahlreiche Grafiken, Verbreitungskarten und Tabellen auf der Basis instruktiver Beispiele tragen mit dazu bei, daß dieses Waldbau-Buch eine echte Fundgrube und ein ausgezeichnetes Nachschlagewerk für Foststudenten und Praktiker ist.

B. R. Stephan (Grosshansdorf)

Farbatlas der Basidiomyceten. (Colour Atlas of Basidiomycetes). 10. Lieferung. Von M. Moser und W. Jülich unter Mitarbeit von C. Furrer-Ziogas. 1992. Gustav Fischer Verlag, Stuttgart und New York. ISBN 3-437-30720-7. 88 Seiten und 56 Farbtafeln. DM 92,—.

Seit 1985 sind 10 Lieferungen des „Farbatlas der Basidiomyceten" erschienen mit Abbildungen von über 1000 Pilzarten. Hinzu kommen inzwischen 103 Gattungsdiagnosen in deutsch, englisch, französisch und italienisch. Sie enthalten Angaben über den Typus male, der Ökologie und der Abgrenzung zu anderen Gattungen, belegt mit den wichtigsten Literaturzitaten. Die über 90, meist der Gattung, etwaige Synonyme sowie Beschreibungen der Merkdurch Studioaufnahmen dargestellten Pilzarten der 10. Lieferung gehören zu den *Polyporales*, *Boletales* sowie überwiegend zu den *Agaricales*. Die Fotografien sind in der Regel gut und eine geeignete Hilfe bei der Bestimmung von Basidiomyceten nach den von denselben Autoren verfaßten Bestimmungsbüchern der „Kleinen Kryptogamenflora", die ebenfalls im G. Fischer-Verlag erschienen ist. Der Farbatlas ist bereits jetzt, obwohl noch Lieferungen ausstehen, ein ausgezeichnetes und empfehlenswertes Werk für jeden Mykologen.

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Genetik. Uni-Taschenbücher 1015. 2. Auflage. Von F. Kaudewitz. 1992. Verlag Eugen Ulmer, Stuttgart. ISBN 3-8252-1015-4. 533 Seiten mit 280 Abbildungen und 16 Tabellen. DM 48,—.

Kaum ein anderes Fachgebiet der Biologie hat in den letzten 10 Jahren eine so explosionsartige Entwicklung durchgemacht wie die Molekulargenetik. So wurde es 9 Jahre nach Erscheinen der 1. Auflage notwendig, dem seitdem enorm angestiegenen Wissen mit der Herausgabe einer erweiterten und überarbeiteten 2. Auflage Rechnung zu tragen. Das vorliegende Buch gliedert sich